MULTIPLE DISTURBANCE INTERACTIONS AND DROUGHT INFLUENCE FIRE SEVERITY IN ROCKY MOUNTAIN SUBALPINE FORESTS

Christof Bigler,[1,2] Dominik Kulakowski, and Thomas T. Veblen

Department of Geography, University of Colorado, Boulder, Colorado 80903 USA

Abstract. Disturbances such as fire, insect outbreaks, and blowdown are important in shaping subalpine forests in the Rocky Mountains, but quantitative studies of their interactions are rare. We investigated the combined effects of past disturbances, current vegetation, and topography on spatial variability of the severity of a fire that burned approximately 4500 ha of subalpine forest during the extreme drought of 2002 in northwestern Colorado. Ordinal logistic regression was used to spatially model fire severity in relation to late 1800s fires, a 1940s spruce beetle outbreak, forest cover type, stand structure, and topography. The late 1800s fires reduced the probability of burning in 2002, and the 1940s beetle outbreak slightly increased the probability of fire, particularly at high severity. Aspen (*Populus tremuloides*) and lodgepole pine (*Pinus contorta*) stands, which established after the late 1800s fires, were less likely to burn, whereas Engelmann spruce (*Picea engelmannii*)–subalpine fir (*Abies lasiocarpa*) stands were more likely to burn. The highest elevations (≥3100 m) had the lowest probability of burning, whereas intermediate elevations (2900–3100 m) had an increased probability of burning at high severity. The influences of the late 1800s fires and 1940s beetle outbreak on stand structure and forest cover type may be more important than their direct effects on fuels. The most important predictors determining fire severity were stand structure, forest cover type, the late 1800s fires, and elevation. Although, in other studies, the effects of pre-burn stand conditions and topography declined with increasingly severe fire weather, in the case of the 2002 fire in Colorado, these predictors explained 42% of the variability of fire severity. Thus, these results suggest that pre-burn stand conditions are important influences on burn severity even for fires burning during extreme drought.

Key words: continuation ratio model; disturbance ecology; fire; GIS (Geographic Information System); insect outbreaks; ordinal logistic regression; robust Huber-White covariance estimator; spatial overlay analysis; statistical modeling; spatial autocorrelation.

INTRODUCTION

Large-scale, severe disturbances such as fire, insect outbreaks, and blowdown are important ecological factors shaping subalpine forest landscapes in the Rocky Mountains (Veblen 2000, Bebi et al. 2003). Infrequent, stand-replacing fires are the main driving factor creating a spatial mosaic of forest patches, which, in turn, affect susceptibility to subsequent disturbances (Romme 1982, Peet 2000, Veblen 2000). Complex interactions among different disturbance types and severities have been widely noted in the forests of the Rocky Mountains (Veblen et al. 1994, Kulakowski and Veblen 2002, Bebi et al. 2003). In many forest types, severe insect outbreaks or blowdowns are believed to either increase (Hopkins 1909, Knight 1987, Everham and Brokaw 1996) or decrease (Knight 1987, McCullough et al. 1998) fire hazard, depending on the importance

attributed to fine fuels in the canopy. Severe fires appear to decrease hazard of subsequent fires for decades or centuries because of fuel reduction (Romme 1982, Lotan et al. 1985).

Following stand-replacing fires in subalpine forests in the Rocky Mountains, quaking aspen (*Populus tremuloides* Michx.) and lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) are often successional to Engelmann spruce (*Picea engelmannii* (Parry) Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt) (Peet 2000). Forest stand structures and species composition, in turn, affect fire behavior. For example, aspen stands can act as fire breaks (van Wagner 1977), young lodgepole pine stands may resist fire better than spruce–fir stands (Despain and Sellers 1977), and flammability of many forest types is believed to increase with stand age (Loope and Gruell 1973). Topography also affects fire behavior both directly, in the form of fire breaks, and indirectly by affecting local climate, forest structure, and composition (Kushla and Ripple 1997, Baker and Kipfmueller 2001). Fire spread and severity across the landscape are strongly influenced by the spatial arrangement of forest patches, topography, ignition points of fires, wind speed, wind direc-

tion, fuel moisture, and relative humidity (Turner and Romme 1994, Baker 2003). However, quantitative research is needed on the combined effects of disturbance history, vegetation, and topography on fire severity in subalpine forests (Odion et al. 2004).

Fire regimes and vegetation patterns are not only controlled by prefire disturbances and topography, but also by regional climatic variability (Bessie and Johnson 1995, Baker 2003, Schoennagel et al. 2004). While the amount of fine and large fuels may be limiting to fire occurrence in open, dry woodlands in the montane zone of the Rocky Mountains, fires in the more mesic subalpine forests may be more dependent on extremely dry weather as opposed to fuel quantity (Veblen 2000, Baker 2003). Furthermore, the strength of the influences of pre-burn stand conditions and topography is believed to decline with increasingly severe fire weather (Turner and Romme 1994, Bessie and Johnson 1995). The relative impact of climate vs. fuels on fire occurrence is also highly debated in other ecosystems such as the chaparral in California (Keeley and Fotheringham 2001, Minnich 2001).

The large and severe 2002 Big Fish Lake fire in the White River National Forest (WRNF) in northwestern Colorado, USA, in combination with previous research on disturbance history in the area presented a unique opportunity to investigate the combined effects of multiple pre-2002 disturbance events, vegetation, and topography on fire severity during extreme drought (Fig. 1, Plate 1 [top]). In the late 1800s (ca. 1879, ca. 1887, and through the 1890s), extensive and severe fires occurred in this and adjacent areas, which were mapped by G. B. Sudworth in 1898 (Sudworth 1900: Fig. 1b). These late 1800s fires were associated with extremely dry weather (Sudworth 1900). In the 1940s, a severe spruce beetle (*Dendroctonus rufipennis* Kirby) outbreak killed over 90% of the spruce timber volume in WRNF, leaving abundant dead fuels (Hinds et al. 1965; see Fig. 1b). However, between 1950 and 1990, lightning-caused fires did not increase in forests affected by spruce beetle outbreaks (Bebi et al. 2003). Ninety-five percent of the observed fires between 1950 and 1990 were <2.1 ha in extent and largely of low severity during this period of less extreme drought than between 1999 and 2002.

Previous work has shown that occurrence of stand-replacing fire reduces susceptibility to spruce beetle outbreaks (Veblen et al. 1994, Bebi et al. 2003, Kulakowski et al. 2003), but no empirical evidence has found that beetle outbreak increases fire hazard during years of normal weather. In this study, the effects of spatial interactions of the late 1800s fires, the 1940s beetle outbreak, stand structures, species composition, and topography (elevation, aspect, slope steepness, curvature) on the severity of the 2002 fire are investigated using overlay analysis and ordinal logistic regression. The severe drought of 1999 to 2002 permits assessment of the relative impact of previous disturbances and oth-

PLATE 1. (Top) Burned forest landscape in the White River National Forest (Colorado) with some unburned aspen stands. (Bottom) Fire behavior changes with stand structure: In the foreground is a forest stand that burned at high severity; a younger, unburned stand is in the background. Photo credits: T. T. Veblen.

er environmental factors on fire severity during extreme drought. In this study, we address the following questions: (1) What is the relative importance of prefire disturbances, stand structure, species composition, and topographic patterns in determining probability of fire severities? (2) Did the late 1800s fires reduce probability of high fire severity? (3) Did the 1940s beetle outbreak affect severity of the 2002 fire following extreme drought?

STUDY AREA AND DATA SETS

Study area

The study area is situated in the Flat Tops Wilderness of WRNF, on a basaltic plateau in northwestern Colorado. The study area extends over 26 320 ha and includes 12 375 ha of forested area of which 4487 ha burned in 2002 (Fig. 1a). The main tree species are Engelmann spruce, subalpine fir, lodgepole pine, and quaking aspen. Elevation ranges between 2500 and 3700 m (Fig. 1d). The closest climate station, Marvine
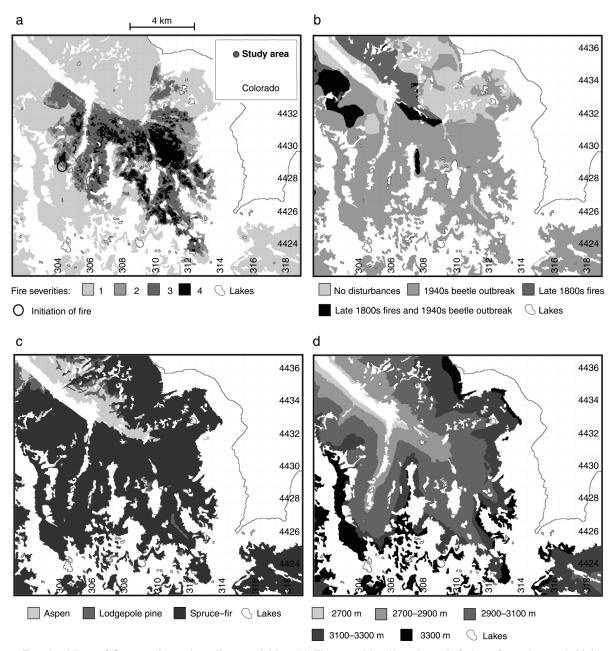
FIG. 1. Maps of fire severity and predictor variables. (a) Fire severities (1, unburned; 2, low; 3, moderate; 4, high). Initiation site of the fire is shown as an open circle; the location of the study area in Colorado is shown at the top right. (b) Prefire disturbances (late 1800s fires, 1940s beetle outbreak, and both). (c) Forest cover type. (d) Elevation (derived from a DEM). The area in the northeast corner is outside of the study area perimeter, delimited by the line. White areas represent nonforest (grassland, shrubland, water, rock, willows). The horizontal and vertical grid lines have a spacing of 1 km. Coordinates are shown as UTM (Universal Transverse Mercator) coordinates (units: 1000 m).

Ranch at 2380 m a.s.l. (above sea level), has a mean January temperature of $-6.8°C$, a mean July temperature of $11.4°C$, and an annual precipitation of 668 mm. A severe state-wide drought began in 1998 which culminated in January to September 2002 being the driest period since 1895 (*data available online*).[3]

Data sets

The data sets were available as or converted to digital raster maps with 30-m resolution. Fire severity data for the 2002 Big Fish Lake fire were provided by the USDA Forest Service and the U.S. Geological Survey and were originally derived from pre- and postfire Landsat TM (Thematic Mapper) imagery, the latter taken shortly after the fire. Fire severity classification was based

on dNBR (Differenced Normalized Burn Ratio; Key and Benson 2005), which was formulated from TM band 4 (near infrared) and band 7 (short-wave infrared) reflectance change. The classification resulted in four categories (Fig. 1a): fire severity 1, unburned; fire severity 2, low severity (surface fire, overstory largely not scorched); fire severity 3, moderate severity (many canopy tree crowns scorched, some green crowns remained); fire severity 4, high severity (all canopy trees killed). The spatial and categorical accuracy of the fire severity map was checked by systematically visiting 13 field sites and making observations en route between each field site. The only discrepancy with field observations was the omission of some burned areas in the western sector from the severity map. The fire burned from late July to late August, and spread largely from west to east.

We used data sets on prefire disturbances, vegetation, and topography to assess their influences on fire severity. Sudworth's map of the late 1800s fires was available as a binary map (burned/unburned; Fig. 1b) (Sudworth 1900, Bebi et al. 2003). Comparison of locations on Sudworth's map with modern topographic maps yielded a mean positional error of 70 m. Furthermore, we used the northern part of the map of the 1940s spruce beetle outbreak (1940s beetle outbreak/no 1940s beetle outbreak; Fig. 1b), which was mapped for spruce–fir forests and field checked by Bebi et al. (2003). Data on forest cover type (aspen, lodgepole pine, spruce–fir; Fig. 1c) and stand structure (1, nonstocked; 2, established seedlings, diameter <2.5 cm; 3, saplings/poles, diameter of most trees 2.5–22.9 cm; 4, mature stands, diameter of most trees >22.9 cm; 5, old-growth stands) as of 1993 were from the USDA Forest Service Resource Information System (RIS). Elevation data from a USGS digital elevation model (DEM; Fig. 1d) were used to derive slope steepness (continuous variable; measured in degrees), east–west aspect derived from sine-transformed aspect (circular, continuous variable with east = +1 and west = −1), north–south aspect derived from cosine-transformed aspect (circular, continuous variable with north = +1 and south = −1), and tangential curvature (continuous variable with values <0 = concave and >0 = convex).

DATA ANALYSIS

Spatial overlay analysis

To assess associations between fire severity and predictor variables, pairwise overlay analyses were performed. Contingency tables were calculated for the observed area of the categories of one predictor variable, which occurred in the four categories of fire severity. Observed areas were compared with expected areas, which were calculated assuming independence between variables (i.e., the proportion of a predictor variable to the total area in each fire severity category; see Zar 1999). GRASS (Geographic Resources Analysis Support System; version 5.3, *available online*)[4] was used to perform GIS (Geographic Information System) analyses.

Models for ordinal responses

Ordinal logistic regression.—Ordinal logistic regression (OLR) makes use of the full range of ordinal data (e.g., fire severity categories) in contrast to the commonly used procedures of binary regression or classification and regression trees (CART). Although ordinal data are not uncommon in ecology, ecological studies have largely neglected the use of specific ordinal regression models (Guisan and Harrell 2000). The main difference from binary logistic regression is that several equations have to be solved simultaneously in OLR. Two distinct OLR models are available for discretized continuous response data: the proportional odds (PO) model (Walker and Duncan 1967), which is based on cumulative probabilities, and the continuation ratio (CR) model (Armstrong and Sloan 1989), which is based on conditional probabilities. We assessed PO and CR model assumptions about ordinality, i.e., the response variable is related in an ordinal way to the predictors (see the graphical methods described in Harrell 2001). These regression diagnostics showed that the ordinality for the CR model held well, which is particularly suitable when observations have to pass through one category to reach the next. Furthermore, smoothed partial residual plots (see Harrell 2001) implied the use of the extended CR model (Armstrong and Sloan 1989), which allows for unequal slopes (i.e., interactions between selected variables and categories of the response variable).

If Y is a categorical response variable with $k + 1$ ordered categories $1, \ldots, k + 1$, then the conditional probabilities of the extended CR model are

$$\Pr(Y = j \mid Y \geq j, X = x)$$

$$= \frac{1}{1 + \exp[\alpha + \theta_j + X(\gamma + \lambda_j)]^{-1}} \quad (1)$$

with $j = 1, 2, \ldots, k$, and $\Pr(Y = k + 1 \mid Y \geq k + 1, X = x) = 1$; α is an overall intercept, $\theta_1 \equiv 0$ and $\theta_2, \ldots, \theta_k$ are cohort increments from α, X contains the predictor variables, γ contains the slopes, and $\lambda_1 \equiv 0$ and $\lambda_2, \ldots, \lambda_k$ are increments from γ that contain cohort × variable interactions. Y belongs to fire severity cohort $1, \ldots, k$, if $Y \geq 1, \ldots, Y \geq k$.

Based on these conditional probabilities (Eq. 1), unconditional probabilities were derived:

$$\Pr(Y = j \mid X = x) = \Pr(Y = j \mid Y \geq j, X = x)$$

$$\times \left[1 - \sum_{i=1}^{j-1} \Pr(Y = i \mid X = x) \right] \quad (2)$$

with $j = 2, \ldots, k + 1$, and $\Pr(Y = 1 \mid X = x) = \Pr(Y = 1 \mid Y \geq 1, X = x)$.
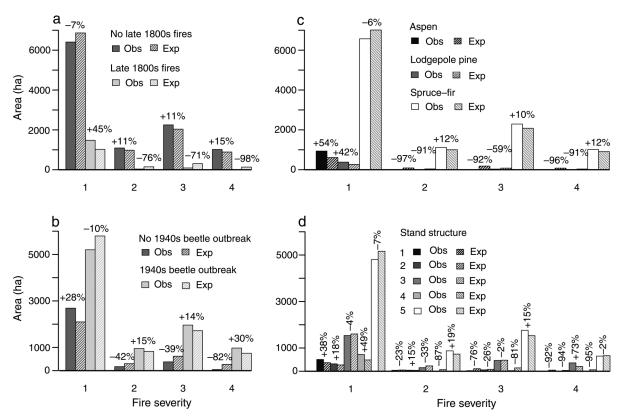
FIG. 2. Spatial overlay analysis of fire severity (1, unburned; 2, low; 3, moderate; 4, high) and predictor variables. Values shown are the observed areas (obs), and expected areas (exp); differences between expected and observed areas are indicated as percentages. (a) Late 1800s fires; (b) 1940s beetle outbreak; (c) forest cover type; (d) stand structure.

Cumulative probabilities, which were used for predictions on the ordinal scale (see *Data analysis: Models for ordinal responses: Model development, interpretation, and evaluation*), were computed as follows:

$$\Pr(Y \geq j \mid X = x) = \sum_{i=j}^{k+1} \Pr(Y = i \mid X = x) \quad (3)$$

with $j = 1, \ldots, k + 1$, and $\Pr(Y \geq 1 \mid X = x) = 1$.

The statistical computing software R (version 1.9.1; R Development Core Team 2003) was used for the computations. The extended CR model was fitted using the R functions lrm() and cr.setup() from the Design package (Harrell 2001). The R package GRASS was used for the exchange of GIS data between GRASS and R.

Adjusting the variances due to spatial autocorrelation.—Due to the spatial autocorrelation of fire severity (Fig. 1a), the assumption of independence of the observations is violated (Legendre 1993, Keitt et al. 2002). Thus, type I errors would be increased in statistical tests (i.e., rejection of the null hypothesis when in fact there is no effect of the predictor variable on the response variable), which would lead to flawed

inferences. To get a working independence model, we applied the robust Huber-White ''sandwich'' covariance estimator (Huber 1967), which is unbiased for cluster-correlated data (Williams 2000). Each homogeneous fire severity patch (i.e., adjacent grid cells of the same fire severity) was treated as a cluster, and the R function robcov() in the Design package was used to correct for correlated responses (Harrell 2001).

Model development, interpretation, and evaluation.—A random sample of 75% of the data ($n = 103\,156$) was used for model development and the remaining 25% ($n = 34\,290$) for model evaluation. Starting with an extended CR model (Eq. 1) that included all predictor variables and cohort $\times$ predictor interactions, we removed variables or interactions based on global test statistics (Harrell 2001). ANOVAs with χ^2 distributed Wald test statistics were computed to remove predictors or sets of predictors with $P \geq 0.1$, starting with the variable with the highest P value. The amount of explained fire severity variability in the final model was assessed based on R^2 (Nagelkerke 1991). The effects of the predictor variables on fire severity are interpreted as conditional probabilities (Eq. 1).

TABLE 1. ANOVA results with global Wald test statistics based on the robust covariance estimator.

Predictor	χ^2	df	P	$\chi^2 - $ df
Cohort	295.18	20	<0.0001	275.18
Late 1800s fires	77.05	3	<0.0001	74.05
1940s beetle outbreak	7.07	1	0.0078	6.07
Forest cover type	110.93	6	<0.0001	104.93
Stand structure	300.93	12	<0.0001	288.93
Elevation	72.00	3	<0.0001	69.00
Slope steepness	24.91	3	<0.0001	21.91
East–west aspect	3.96	1	0.0465	2.96
Tangential curvature	39.03	1	<0.0001	38.03
Cohort × late 1800s fires	12.17	2	0.0023	10.17
Cohort × forest cover type	77.72	4	<0.0001	73.72
Cohort × stand structure	17.96	8	0.0215	9.96
Cohort × elevation	5.40	2	0.0671	3.40
Cohort × slope steepness	14.75	2	0.0006	12.75
Total interaction	238.36	18	<0.0001	220.36
Total	2139.74	32	<0.0001	

Notes: Values shown are the partial χ^2 values, df (degrees of freedom), and P values for significant predictors (including cohort interactions) and cohort × predictor interactions ($n = 103\,156$ observations); $\chi^2 - $ df shows the relative importance of the predictors. The variable cohort includes cohort increments and cohort interactions (see Eq. 1). Cohorts include observations of a certain fire severity category and higher.

Odds ratios, conditional on fire severity cohort j, were derived to assess the effects of the predictors (for detailed explanations see Appendix A).

To make predictions on the original, ordinal scale and to evaluate the model empirically, the cumulative probabilistic predictions (Eq. 3) were recoded (see Appendix B). To assess accuracy of predictions, a contingency table for observed and predicted fire severities was derived from the evaluation data set, and the γ statistic was calculated, a measure of association for ordinal data (Goodman and Kruskal 1954). Finally, spatial predictions were made by applying the extended CR model to all grid cells in the forested area.

RESULTS

Spatial overlay analysis

The late 1800s fires decreased the probability of burning in 2002; a 45% larger than expected area was observed not to burn (Figs. 1a, 1b, and 2a). Beetle-attacked stands burned more often than expected, particularly at high fire severity (+30%; Figs. 1a, 1b, and 2b). Aspen and lodgepole pine stands were in the unburned category more than expected (+54% and +42%, respectively), and spruce–fir stands had higher than expected extents in the low to high fire severity categories (Figs. 1a, 1c, and 2c). Young stands (stand structure 1 and 2) and stand structure 4 were more likely not to burn (stand structure 1, +38%; 2, +18%; 4, +49%), whereas old-growth stands (stand structure 5) increased the probability of burning at low or moderate severity (+19% and +15%; Fig. 2d). Stand structure 3 was found much more often than expected in the highest fire severity category (+73%). Higher elevations (≥3100 m) had an increased likelihood of not

being burned in 2002 compared to lower elevations (results for all variables are shown in Appendix C, Table C1). Elevations below 2900 m most likely burned at moderate fire severity (+47%), and elevations between 2900 and 3100 m were found much more often than expected in the highest fire severity category (+106%; Fig. 1a, d). Flat terrain (0–10° slope steepness) did not burn (+5%) or more likely burned at high fire severity (+22%), and steep terrain (≥20°) was more likely to burn at low severity (+33%) or moderate severity (+41%). North aspects were more likely to show moderate severity (+28%) and high fire severity (+15%), whereas south aspects were more likely not to burn (+10%) or burned at low severity (+6%). East-west aspects showed the largest difference in the low fire severity category, where west aspects were more prevalent (+7%) than east aspects (−9%). The largest effects for tangential curvature were found in the high fire severity category, where concave and convex sites burned less often than expected (−16% and −6%, respectively), whereas terrain with low curvature was observed more often (+6%) than expected in the high severity category.

Relative importance of predictors

Based on the ANOVA table of the extended CR model (Table 1, Eq. 1), the relative importance of predictors or sets of predictors and cohort interactions was calculated with $\chi^2 - $ df (Harrell 2001). In decreasing order, the relative importance of predictors that significantly influenced fire severity was: stand structure ($\chi^2 - $ df = 288.93), forest cover type (104.93), late 1800s fires (74.05), elevation (69.00), tangential curvature (38.03), slope steepness (21.91), 1940s beetle outbreak (6.07),

TABLE 2. Extended continuation ratio model.

Predictor variable	Coefficients	SE (naive)	SE (robust)	Wald Z	P
α: intercept	−10.596	0.187	3.318	−3.19	0.001
θ_2: cohort $y \geq 2$	−4.979	0.427	6.969	−0.71	0.475
θ_3: cohort $y \geq 3$	14.999	0.521	9.393	1.60	0.110
γ: late 1800s fires	2.734	0.040	0.346	7.89	0.000
γ: 1940s beetle outbreak	−0.726	0.017	0.273	−2.66	0.008
γ: fct lodgepole pine	−2.105	0.104	1.085	−1.94	0.052
γ: fct spruce–fir	−5.262	0.087	0.704	−7.47	0.000
γ: stand structure 2	−1.264	0.066	0.583	−2.17	0.030
γ: stand structure 3	−2.015	0.054	0.262	−7.68	0.000
γ: stand structure 4	0.885	0.078	0.608	1.46	0.146
γ: stand structure 5	−0.865	0.050	0.354	−2.44	0.015
γ: elevation	0.006	0.000	0.001	5.09	0.000
γ: slope steepness	−0.047	0.001	0.011	−4.41	0.000
γ: east–west aspect	0.261	0.008	0.131	1.99	0.046
γ: tangential curvature	−20.381	1.776	3.262	−6.25	0.000
λ_2: cohort $y \geq 2 \times$ late 1800s fires	−1.851	0.093	0.546	−3.39	0.001
λ_3: cohort $y \geq 3 \times$ late 1800s fires	0.173	0.194	0.886	0.20	0.845
λ_2: cohort $y \geq 2 \times$ fct lodgepole pine	1.191	0.319	0.926	1.29	0.199
λ_3: cohort $y \geq 3 \times$ fct lodgepole pine	2.664	0.323	2.254	1.18	0.237
λ_2: cohort $y \geq 2 \times$ fct spruce–fir	6.086	0.248	0.736	8.27	0.000
λ_3: cohort $y \geq 3 \times$ fct spruce–fir	4.896	0.246	1.714	2.86	0.004
λ_2: cohort $y \geq 2 \times$ stand structure 2	1.090	0.135	1.244	0.88	0.381
λ_3: cohort $y \geq 3 \times$ stand structure 2	3.074	0.329	1.631	1.88	0.060
λ_2: cohort $y \geq 2 \times$ stand structure 3	1.228	0.113	0.558	2.20	0.028
λ_3: cohort $y \geq 3 \times$ stand structure 3	1.240	0.205	0.776	1.60	0.110
λ_2: cohort $y \geq 2 \times$ stand structure 4	−0.276	0.184	1.035	−0.27	0.789
λ_3: cohort $y \geq 3 \times$ stand structure 4	0.794	0.310	1.858	0.43	0.669
λ_2: cohort $y \geq 2 \times$ stand structure 5	0.432	0.106	0.686	0.63	0.529
λ_3: cohort $y \geq 3 \times$ stand structure 5	0.914	0.202	0.916	1.00	0.318
λ_2: cohort $y \geq 2 \times$ elevation	−0.001	0.000	0.002	−0.42	0.675
λ_3: cohort $y \geq 3 \times$ elevation	−0.007	0.000	0.003	−2.32	0.020
λ_2: cohort $y \geq 2 \times$ slope steepness	0.029	0.002	0.018	1.66	0.096
λ_3: cohort $y \geq 3 \times$ slope steepness	0.105	0.002	0.030	3.50	0.000

Notes: Values shown are the fitted regression coefficients (including incremental coefficients; see Eq. 1); standard errors (SE, ''naive'' estimation with spatial autocorrelation not taken into account; adjusted ''robust'' estimation with spatial autocorrelation taken into account); Wald Z test statistic (''robust''); P values (''robust''); $n = 103\,156$ observations; fct = forest cover type. The symbols α, θ_2, θ_3, γ, λ_2, and λ_3 correspond to the symbols in Eq. 1.

and east–west aspect (2.96). Total cohort interactions were significant ($P < 0.0001$), which is consistent with the relaxation of the equal slopes assumption of the CR model (Eq. 1).

Model estimates, inferences and predictions

Most of the predictor variables affected fire severity significantly (γ in Table 2 and Eq. 1), and some of the cohort $\times$ predictor interactions were significant as well (λ in Table 2 and Eq. 1). Applying the robust covariance estimator greatly increased standard errors (Table 2). Multicollinearity among variables did not seriously affect the validity of the model, since Spearman's rank correlations ranged from −0.4 to 0.57. The predictor variables included in the model explained 42% of the variability in fire severity.

After a late 1800s fire, a stand was 15.4 times more likely not to burn in 2002 (based on odds ratios), low severity fire (fire severity 2) was 2.4 times more likely to occur conditional on cohort 2 (i.e., fire severities ≥2), and moderate severity fire (fire severity 3) was 18.3 times more likely conditional on cohort 3 (i.e., fire severities ≥3). In the following text, the conditional

statements will not be repeated. Beetle outbreaks reduced the odds in all fire severity categories by 0.5 times (i.e., beetle-attacked stands had a two times higher risk to burn at higher severity). Compared with aspen stands, lodgepole pine stands were 0.12 times and spruce–fir stands 0.005 times less likely to be in the unburned category (i.e., aspen stands are 200 times more likely not to burn than spruce–fir stands). At low fire severities, the odds decreased for lodgepole pine by 0.4 and increased for spruce–fir by 2.3, and at moderate severities, lodgepole pine was 1.7 times and spruce–fir 0.7 times as likely as aspen to burn. Compared with stand structure 1, the likelihood of not burning was decreased for stand structure 2 (0.28), stand structure 3 (0.13), and stand structure 5 (0.42), and increased for stand structure 4 (2.42). For stand structure 5, the odds for low severity decreased (0.65) and increased slightly for moderate severity (1.05). An elevational gain of 100 m resulted in a 1.8 times higher likelihood not to burn, a 1.64 times higher likelihood to burn at low severity, and a 0.9 times lower likelihood to burn at moderate severity. For effects of the remaining topographic variables see Table 2.
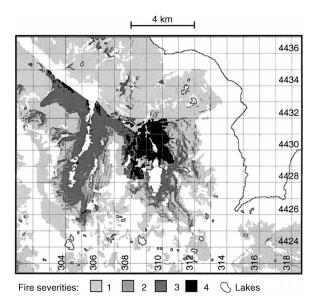
FIG. 3. Spatial predictions of fire severity (1, unburned; 2, low; 3, moderate; 4, high) based on the extended continuation ratio model.

Comparing observed and predicted fire severities, the evaluation of the model resulted in a relatively high γ (0.71) based on the contingency table of the evaluation data set (Appendix D, Table D1). For the evaluation data set, 12 415 grid cells were observed to burn (fire severities 2–4), whereas 10 679 grid cells were predicted to burn. Applying the model to all grid cells, the general pattern of the fire is relatively well depicted; however, fire severity 3 was predicted more often between approximately 2900 and 3100 m, and less often between approximately 3100 and 3300 m (Figs. 1a, 1d, and 3).

DISCUSSION

Ecologists are increasingly aware of patterns that are spatially structured at different scales, which require spatial analysis to reveal spatial structure (Lichstein et al. 2002, Liebhold and Gurevitch 2002). However, failure to account for autocorrelation can lead to seriously flawed conclusions as noted in numerous studies (Keitt et al. 2002, Legendre et al. 2002, Diniz-Filho et al. 2003). In our landscape-scale study of ordinal fire severity data, adjusting the covariance matrix resulted in much higher standard errors (see also Fahrmeir and Pritscher 1996), which affected both model development and inference (Tables 1 and 2). Using observations sampled sufficiently distant from each other—as has been suggested in some studies—is not recommended, since it would reduce sample size strongly and would neglect local-scale variability (Legendre 1993, Lichstein et al. 2002).

Modeling fire severities using OLR proved to be a useful approach in our spatial setting. Instead of recoding ordinal data as binary or nominal data and thus

losing information, the original ordinal data should be analyzed (for some examples, see Schabenberger 1995, Weatherspoon and Skinner 1995, Fahrmeir and Pritscher 1996, Guisan et al. 1998, Guisan and Harrell 2000). Unlike bivariate overlay analysis, where only one relationship is analyzed at a time (Fig. 2), regression models allow predictions, simultaneous testing of hypotheses, and assessment of effects.

Vegetation patterns, as represented by stand structure and forest cover type, had by far the largest impact on fire severity, followed by the late 1800s fires and elevation (Table 1). The 1940s beetle outbreak and other topographic variables seemed to be less important. However, several of the predictors showed significant interactions with different fire severities. The apparently low importance of the variables late 1800s fires and 1940s beetle outbreak requires further explanation. Stands that burned in the late 1800s have an increased probability to be stand structure 2 (+95%) or 3 (+164%), and a much higher probability to be aspen (+403%) and lodgepole pine (+311%) (Appendix C, Table C2; see also Kulakowski et al. 2004). Beetle-affected stands are obviously in the spruce–fir cover type and have a higher probability to have stand structures 4 (+28%) or 5 (+8%). Thus, past disturbance by fire or beetle outbreak strongly determine forest cover type and stand structure which were identified in ordinal logistic regression as strong predictors of fire severity.

Occurrence of late 1800s fire strongly decreased fire severity (Fig. 2a, Table 2), which supports earlier findings that a previous fire may reduce the hazard of subsequent fire (Romme 1982, Lotan et al. 1985). Although occurrence of stand structure 3 might suggest increased flammability (Fig. 2d), the reduced flammability of stands that burned in the late 1800s (Fig. 2a) is mainly attributable to the fire-resistant aspen and to a lesser extent lodgepole pine cover types (Table 2). Stands that were affected by the 1940s outbreak were more likely to burn at high fire severity (Fig. 2b, Table 2). However, why was the variable late 1800s fires more important than the variable 1940s beetle outbreak? Whereas the late 1800s fires dramatically changed stand structure and forest cover type to conditions less conducive to severe fire, a spruce beetle outbreak does not change cover type and may not even result in a detectable change in stand structure because beetle outbreaks only attack older stands. In fact, the extent of the 1940s beetle outbreak was very strongly influenced by the late 1800s fires, which greatly reduced susceptibility to outbreak (Veblen et al. 1994, Bebi et al. 2003, Kulakowski et al. 2003). The 1940s beetle outbreak increased the amount of large dead fuels and shifted canopy dominance from the host species spruce towards the nonhost species fir (Veblen et al. 1991). However, in comparison with effects of a severe fire which eliminates all fine fuels and radically changes stand structures, these are relatively minor changes in the

amount of live and dead large fuels. The main explanation for greater fire severity in beetle-affected stands is probably the greater occurrence of beetle outbreaks in older stands (Veblen et al. 1991) with an abundance of different fuel sizes (both dead and alive) and laddered fuel structures. In addition, dead or decaying fuels desiccate faster during sustained drought and more readily release flammable compounds (Knight 1987). Thus, the large quantity of beetle-killed trees still standing in 2002 probably also contributed to increased fire severity in this cover type.

Some of our results may partly reflect varying spatial accuracy and resolution of the input data sets. We compared the Sudworth map (Sudworth 1900) with a fine resolution map of the late 1800s fires based on tree-ring reconstructions in the western one-third of our study area (Kulakowski et al. 2003). The fine resolution map did not detect evidence of fire in a ~400-ha area of spruce–fir stands mapped by Sudworth as being burned in the late 1800s. Given the high overall accuracy of the Sudworth map found in field checks for this study and broader scale studies (Bebi et al. 2003, Kulakowski et al. 2004), we suspect that this discrepancy reflects patchy and/or lower severity burning within a larger perimeter mapped as burned. Even in the case of the 2002 fire, field observations revealed that a ~300-ha patch of mainly old-growth spruce–fir forests in the western part of the study area which had been mapped as unburned on the fire-severity map did in fact burn. However, this patch burned only to the boundary of the late 1800s fires as mapped by Kulakowski et al. (2003). Given these considerations, the relative importance of the late 1800s fires would not change, since the errors of the maps of the late 1800s fires and the 2002 fire would cancel out. However, the relative importance of the 1940s beetle outbreak would slightly increase, if the patch would have been mapped as burned in 2002. In addition, the effect of spruce–fir and old-growth forests might be higher. However, even with these potential sources of error, it is clear that previous disturbances affected the severity of the 2002 fire, and that the relative importance of the late 1800s fires was greater than the 1940s beetle outbreak.

Some studies have observed or postulated increased flammability of coniferous forests following spruce beetle outbreaks (Hopkins 1909, Knight 1987). On the other hand, in northwestern Colorado after the 1940s beetle outbreak, fire did not increase in beetle-affected stands compared to unaffected spruce–fir stands over the period 1950 to 1990 (Bebi et al. 2003). In fact, in the case of one low severity fire, the spread of the fire was less in beetle-attacked stands than in adjacent unaffected stands (Kulakowski 2003). The consequences of a spruce beetle outbreak for subsequent fire occurrence appear to depend greatly on the occurrence of extreme drought such as the 1999–2002 drought that preceded the Big Fish Lake fire. The 1950–1990 period was not characterized by a similar drought, and there-fore, only small, low-severity fires occurred in this period (Bebi et al. 2003, Kulakowski et al. 2003). Following beetle outbreaks, the increased amount of dead fine fuels may increase flammability in a stand for a few years (Knight 1987). However, following the decay of the fine fuels, overall fire hazard may actually decrease for decades due to the increased moisture related to the development of mesic understory vegetation in subalpine forests (Stocks 1987) and lack of continuous fine fuel in the canopy (Knight 1987). Beetle outbreaks in the subalpine forests of the Rocky Mountains apparently must be followed by exceptional fire conditions such as extreme drought and strong winds, in order for the increased amount of large, dead fuels to result in increased fire severity.

Forest cover type affects fire spread and severity in the mesic, subalpine forests of the Rocky Mountains. Spruce–fir stands have the highest probability of being burned at high fire severity (Fig. 2c, Table 2). Particularly aspen, but also lodgepole pine have a lower probability than spruce–fir of being burned (see also Despain and Sellers 1977, Knight 1987). However, flammability of lodgepole pine might be underestimated in our study, since a large part of the lodgepole pine cover type was protected by a large aspen patch that acted as fire break (Fig. 1). Nevertheless, some small aspen patches burned in the 2002 fire (Appendix C, Table C1). Aspen and lodgepole pine stands established after the late 1800s fires (Appendix C, Table C2; Fig. 1). Aspen trees have a higher moisture content, and grow in stands with a mesophytic understory, which decreases fire hazard (van Wagner 1977, Peet 2000). Unlike lodgepole pine, spruce and fir trees retain their lower branches, resulting in increased fire severity due to greater vertical fine fuel continuity (Romme 1982, Baker 2003).

Large and fine fuels generally increase from young to old stands (Baker 2003). Young conifer stands can act as potential fire breaks (Despain and Sellers 1977), however, during the Yellowstone fire in 1988, such stand-age boundaries did not stop the spread of fire (Turner et al. 1994, Turner and Romme 1994, Schoennagel et al. 2004). During the 2002 Big Fish Lake fire, spruce–fir stands that were not stocked or contained only seedlings were found within or adjacent to the fire boundary and acted as fire breaks or burned with low or moderate fire severity (map not shown; see Plate 1 [bottom]). These young stands have a higher probability not to burn, and old-growth stands have the highest probability to burn at low or moderate severity (Fig. 2d, Table 2). Higher fire severity in older stands has also been observed by Despain and Sellers (1977). Under extreme fire weather, as in our study, stands with saplings/poles (stand structure 3) had the highest probability to burn at high fire severity, probably because of the dense stocking, the very high vertical fuel continuity, and due to the particular spatial configuration. Mature stands were underrepresented in the burned

area, and the remaining stands were surrounded by grassland, rock, or young stands that did not burn in 2002. Additionally, the 2002 fire spread from west to east, and mature stands grew mostly in the west of the fire origin.

Baker (2003) hypothesized an elevational gradient of climate–fuels interactions from pygmy conifer woodlands to subalpine forests. Over a smaller elevational range, we found that different elevations had different effects on fire severities. The highest elevations ($\geq$3100 m) have the lowest probability to burn, whereas intermediate elevations (2900–3100 m) have the highest probability to burn at high severity (Appendix C, Table C1; Table 2). Weatherspoon and Skinner (1995) also observed decreasing fire severities with increasing elevation. Increasing moisture and cooler temperatures may explain the reduction of high fire severity at the highest elevations.

Including significant variables and fire severity cohort $\times$ variable interactions, 42% of the variability of fire severity could be explained by pre-burn stand conditions and topography. Considering the complexity of the environment–fire relationship, the model predictions were relatively accurate ($\gamma = 0.71$). However, the spatial application of the model on the landscape should be considered as a risk map rather than as a predictive map, since the dynamic behavior of the fire is not considered in our empirical model. The susceptibility of any particular forest stand to being burned is determined by the occurrence and severity of fire in adjacent stands (Knight 1987, Turner and Romme 1994), but fire severity in neighboring grid cells is not known beforehand. A more mechanistic model should also include ignition point, wind speed, and direction, as well as fuel moisture, but these local factors are generally not known before the fire (Gardner et al. 1999).

Conclusions

Although it has been argued that the effects of regional weather patterns on fire behavior are sometimes so dominant that fire behavior does not vary strongly with ecosystem properties that affect fuel loads and structure (Bessie and Johnson 1995), in our study, local ecosystem factors strongly influenced fire severity even under the extreme fire weather of 2002. Our study consistently suggests that prefire disturbances, stand structure, species composition, and topography are important influences on burn severity, and explain a considerable amount of variability. However, extreme drought is needed for a severe fire to spread in these subalpine forests. These results agree largely with the conceptual model of Romme and Despain (1989), whereby weather variability only affects fire when fuel buildup is sufficient. The higher proportion of aspen, spruce–fir, and young stands in our study and the occurrence of a spruce beetle outbreak might explain the differences to the findings of Bessie and Johnson (1995) for more

uniform boreal forests. For the large 1988 Yellowstone fire, the effects of fuels and topography on fire behavior are believed to decline with increasingly severe fire weather (Turner et al. 1994, Turner and Romme 1994). The apparently smaller influence of local biotic and abiotic factors on the Yellowstone fire may also reflect the less extreme elevational gradients, which affected wind speed and direction, and the dominance of mainly lodgepole pine in the Yellowstone National Park.

In our study area, the late 1800s fires decreased fuel loads and strongly reduced fire severity in the 2002 Big Fish Lake fire. The late 1800s fires also greatly reduced susceptibility to the 1940s beetle outbreak. In 2002, beetle-affected stands, where mainly fuel quality changed from live to dead trees, had a slightly higher probability to burn more severely. However, the late 1800s fires were more important than the 1940s beetle outbreak. More important than their direct effects on fuels were their effects on vegetation, particularly on stand structure, but also on species composition. Aspen and lodgepole pine were relatively resistant to fire, and spruce–fir forests experienced increased fire severity. Young stands showed reduced flammability, whereas stands with saplings/poles and old-growth stands tended to burn at higher severity. Topography also affected fire severity, probably both directly and also via influences on vegetation and prefire disturbances.

Our spatial study contributes to a better comprehension of the relative importance and the combined effects of fire and beetle outbreak, vegetation, and topography on fire severity during extreme drought. Previous research in subalpine forests in Colorado has shown the importance of prior occurrence of disturbances such as fire, spruce beetle outbreaks and blowdown to subsequent probability of a stand being affected by beetle outbreak or fire (Veblen et al. 1994, Kulakowski and Veblen 2002, Bebi et al. 2003). The current study further develops that line of research by demonstrating the importance of disturbance history to the severity of subsequent fires. Understanding the spatiotemporal effects of climatic variability on large and severe disturbances, and quantifying interactions among multiple disturbances would contribute further to assess the relative importance of ecosystem properties under different climate scenarios.

Literature Cited

Armstrong, B. G., and M. Sloan. 1989. Ordinal regression models for epidemiologic data. American Journal of Epidemiology **129**:191–204.

Baker, W. L. 2003. Fires and climate in forested landscapes of the U.S. Rocky Mountains. Pages 120–157 *in* T. T. Veblen, W. L. Baker, G. Montenegro, and T. W. Swetnam, editors. Fire and climatic change in temperate ecosystems of the Western Americas. Springer-Verlag, New York, New York, USA.

Baker, W. L., and K. F. Kipfmueller. 2001. Spatial ecology of pre-Euro-American fires in a southern Rocky Mountain subalpine forest landscape. Professional Geographer **53**: 248–262.

Bebi, P., D. Kulakowski, and T. T. Veblen. 2003. Interactions between fire and spruce beetles in a subalpine Rocky Mountain forest landscape. Ecology **84**:362–371.

Bessie, W. C., and E. A. Johnson. 1995. The relative importance of fuels and weather on fire behavior in subalpine forests. Ecology **76**:747–762.

Despain, D. G., and R. E. Sellers. 1977. Natural fire in Yellowstone National Park. Western Wildlands **4**:20–24.

Diniz-Filho, J. A. F., L. M. Bini, and B. A. Hawkins. 2003. Spatial autocorrelation and red herrings in geographical ecology. Global Ecology and Biogeography **12**:53–64.

Everham, E. M., and N. V. L. Brokaw. 1996. Forest damage and recovery from catastrophic wind. Botanical Review **62**: 113–185.

Fahrmeir, L., and L. Pritscher. 1996. Regression analysis of forest damage by marginal models for correlated ordinal responses. Environmental and Ecological Statistics **3**:257–268.

Gardner, R. H., W. H. Romme, and M. G. Turner. 1999. Predicting forest fire effects at landscape scales. Pages 163–185 *in* D. J. Mladenoff, and W. L. Baker, editors. Spatial modeling of forest landscapes: approaches and applications. Cambridge University Press, Cambridge, UK.

Goodman, L. A., and W. H. Kruskal. 1954. Measures of association for cross classification. Journal of the American Statistical Association **49**:732–764.

Guisan, A., and F. E. Harrell. 2000. Ordinal response regression models in ecology. Journal of Vegetation Science **11**:617–626.

Guisan, A., J.-P. Theurillat, and F. Kienast. 1998. Predicting the potential distribution of plant species in an alpine environment. Journal of Vegetation Science **9**:65–74.

Harrell, F. E. 2001. Regression modeling strategies. Springer-Verlag, New York, New York, USA.

Hinds, T. E., F. G. Hawksworth, and R. W. Davidson. 1965. Beetle-killed Engelmann spruce: its deterioration in Colorado. Journal of Forestry **63**:536–542.

Hopkins, A. D. 1909. Practical information on the Scolytid beetles of North American forests. I. Bark beetles of the Genus *Dendroctonus*. Technical report, USDA Bureau of Entomology Bulletin 83. U.S. Government Printing Office, Washington, D.C., USA.

Huber, P. J. 1967. The behavior of maximum likelihood estimates under nonstandard conditions. Pages 221–233 *in* Proceedings of the fifth Berkeley symposium in mathematical statistics. Volume 1. University of California Press, Berkeley, California, USA.

Keeley, J. E., and C. J. Fotheringham. 2001. Historic fire regime in Southern California shrublands. Conservation Biology **15**:1536–1548.

Keitt, T. H., O. N. Bjørnstad, P. M. Dixon, and S. Citron-Pousty. 2002. Accounting for spatial pattern when modeling organism-environmental interactions. Ecography **25**: 616–625.

Key, C. H., and N. C. Benson. 2005. Landscape assessment: ground measure of severity, the Composite Burn Index and remote sensing of severity, the Normalized Burn Ratio. *In* D. C. Lutes, R. E. Keane, J. F. Caratti, C. H. Key, N. C. Benson, S. Sutherland, and L. J. Gangi, editors. FIREMON: fire effects monitoring and inventory system. General Technical Report RMRS-GTR-XXX-CD. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA, *in press.*

Knight, D. H. 1987. Parasites, lightning, and the vegetation mosaic in wilderness landscapes. Pages 59–83 *in* M. G. Turner, editor. Landscape heterogeneity and disturbance. Springer-Verlag, New York, New York, USA.

Kulakowski, D., and T. T. Veblen. 2002. Influences of fire history and topography on the pattern of a severe wind blowdown in a Colorado subalpine forest. Journal of Ecology **90**:806–819.

Kulakowski, D., T. T. Veblen, and P. Bebi. 2003. Effects of fire and spruce beetle outbreak legacies on the disturbance regime of a subalpine forest in Colorado. Journal of Biogeography **30**:1445–1456.

Kulakowski, D., T. T. Veblen, and S. Drinkwater. 2004. The persistence of quaking aspen (*Populus tremuloides*) in the Grand Mesa area, Colorado. Ecological Applications **14**: 1603–1614.

Kushla, J. D., and W. J. Ripple. 1997. The role of terrain in a fire mosaic of a temperate coniferous forest. Forest Ecology and Management **95**:97–107.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology **74**:1659–1673.

Legendre, P., M. R. T. Dale, M. J. Fortin, J. Gurevitch, M. Hohn, and D. Myers. 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. Ecography **25**:601–615.

Lichstein, J. W., T. R. Simons, S. A. Shriner, and K. E. Franzreb. 2002. Spatial autocorrelation and autoregressive models in ecology. Ecological Monographs **72**:445–463.

Liebhold, A. M., and J. Gurevitch. 2002. Integrating the statistical analysis of spatial data in ecology. Ecography **25**: 553–557.

Loope, L. L., and G. E. Gruell. 1973. The ecological role of fire in the Jackson Hole area, northwestern Wyoming. Quaternary Research **3**:425–443.

Lotan, J. E., J. K. Brown, and L. F. Neuenschwander. 1985. Role of fire in lodgepole pine forests. Pages 133–152 *in* D. M. Baumgartner, R. G. Krebill, J. T. Arnott, and G. F. Weetman, editors. Lodgepole pine: the species and its management. Washington State University Cooperative Extension Service, Pullman, Washington, USA.

McCullough, D. G., R. A. Werner, and D. Neumann. 1998. Fire and insects in northern and boreal forest ecosystems of North America. Annual Review of Entomology **43**:107–127.

Minnich, R. A. 2001. An integrated model of two fire regimes. Conservation Biology **15**:1549–1553.

Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. Biometrika **78**:691–692.

Odion, D. C., E. J. Frost, J. R. Strittholt, H. Jiang, D. A. Dellasala, and M. A. Moritz. 2004. Patterns of fire severity and forest conditions in the Western Klamath Mountains, California. Conservation Biology **18**:927–936.

Peet, R. K. 2000. Forests of the Rocky Mountains. Pages 63–102 *in* M. G. Barbour and W. D. Billings, editors. North American terrestrial vegetation. Cambridge University Press, New York, New York, USA.

R Development Core Team. 2003. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 〈http://www.r-project.org〉

Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs **52**:199–221.

Romme, W. H., and D. G. Despain. 1989. The long history of fire in the Greater Yellowstone Ecosystem. Western Wildlands **15**:10–17.

Schabenberger, O. 1995. The use of ordinal response methodology in forestry. Forest Science **41**:321–336.

Schoennagel, T., T. T. Veblen, and W. H. Romme. 2004. The interaction of fire, fuels and climate across Rocky Mountain forests. BioScience **54**:661–676.

Stocks, B. J. 1987. Fire potential in the spruce budworm-damaged forests of Ontario. Forestry Chronicle **63**:8–14.

Sudworth, G. B. 1900. White River Plateau Timber Land Reserve. Pages 117–179 *in* Twentieth annual report of the United States Geological Survey, 1898–1899. Part V. Forest Reserves. U.S. Government Printing Office, Washington, D.C., USA.

Turner, M. G., W. W. Hargrove, R. H. Gardner, and W. H. Romme. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. Journal of Vegetation Science **5**:731–742.

Turner, M. G., and W. H. Romme. 1994. Landscape dynamics in crown fire ecosystems. Landscape Ecology **9**:59–77.

van Wagner, C. E. 1977. Conditions for the start and spread of crown fires. Canadian Journal of Forest Research **7**:23–34.

Veblen, T. T. 2000. Disturbance patterns in southern Rocky Mountain forests. Pages 31–54 *in* R. L. Knight, F. W. Smith, S. W. Buskirk, W. H. Romme, and W. L. Baker, editors. Forest fragmentation in the southern Rocky Mountains. University Press of Colorado, Boulder, Colorado, USA.

Veblen, T. T., K. S. Hadley, E. M. Nel, T. Kitzberger, M. Reid, and R. Villalba. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. Journal of Ecology **82**:125–135.

Veblen, T. T., K. S. Hadley, M. S. Reid, and A. J. Rebertus. 1991. The response of subalpine forests to spruce beetle outbreak in Colorado. Ecology **72**:213–231.

Walker, S. H., and D. B. Duncan. 1967. Estimation of the probability of an event as a function of several independent variables. Biometrika **54**:167–179.

Weatherspoon, C. P., and C. N. Skinner. 1995. An assessment of factors associated with damage to tree crowns from the 1987 wildfires in northern California. Forest Science **41**:430–451.

Williams, R. L. 2000. A note on robust variance estimation for cluster-correlated data. Biometrics **56**:645–646.

Zar, J. H. 1999. Biostatistical analysis. Fourth edition. Prentice-Hall, Upper Saddle River, New Jersey, USA.

APPENDIX A

A discussion of interpreting odds ratios of the extended continuation ratio model is available in ESA's Electronic Data Archive: *Ecological Archives* E086-164-A1.

APPENDIX B

A discussion of recoding the cumulative probabilities to the ordinal scale is available in ESA's Electronic Data Archive: *Ecological Archives* E086-164-A2.

APPENDIX C

Contingency tables from spatial overlay analyses are available in ESA's Electronic Data Archive: *Ecological Archives* E086-164-A3.

APPENDIX D

A comparison of observed and predicted fire severities is available in ESA's Electronic Data Archive: *Ecological Archives* E086-164-A4.